CONTRIBUTIONS TO THE KNOWLEDGE OF THE REPTILES OF THE KARROO FORMATION.

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2. The Lower Jaw of *Lystrosaurus*.

While describing the skull of *Lystrosaurus Putterilli* many difficulties were encountered through the fact that our knowledge of the lower jaw of *Lystrosaurus* is still in a very unsatisfactory state. It was necessary before proceeding any further with this fossil, especially its lower jaw, of which only two disconnected portions are visible, to study the elements of this part and their exact relations in other specimens.

The following is a review of what had been made known before on this subject. I could not go further back than 1855, because Owen's previous work could not be obtained.

Owen only mentions the dentary in the description of *Dicynodon tigriceps* (**1**). A low, obtuse, longitudinal ridge projects from this bone, corresponding with the one on the premaxillary. There are two ridges separated by a groove on the upper border of the left ramus. The groove gradually deepens backwards (for so far present). There is another ridge on the outside of the rami and a vacuity further backwards.

Huxley adds to this in 1859 that there are three ridges on the symphysis, which fit into grooves on the palatal surface of the premaxillary. These ridges are separated from each other by deep grooves. The upper border of the dentary is broad, and is formed by a thick inner and a thin outer wall, separated by a groove. The thick inner wall becomes thinner downwards and reaches the opercular. The surangular is covered by the outer wall. The opercular elements are united in the symphysis.

Owen contributes further to the knowledge of this subject in 1860 in the description of *Lystrosaurus latirostris* (**3**, p. 53):—The lower jaw is continued backwards for a small distance behind the articulation with the quadrate. The articulation surface is hollow. It was impossible to distinguish the angular, surangular, and articular from each other. Angular and surangular diverge forwards. The angular forms the hind and lower boundary of the vacuity in the outside of the jaw. The fore part of the vacuity is formed by a bifurcation of the dentary element. The angular is wedged in between the opercular and the dentary in the symphysial region. The ridge on the outside of the dentary subsides forwards at the vertical channel upon the side of the symphysis, which receives the corresponding tusk when the mouth is shut.

In 1862, while describing *L. Alfredi* (**4**, p. 458), Owen states that he is still unable to distinguish the articular from the surangular. There is no coronoidal process and no complementary. The longitudinal ridge on the outside of the dentary parallels that formed by the canine alveolus of the maxillary.

Owen described the lower jaw of *Oudenodon brevirostris* in 1876 (**5,** p. 58). He states there that the angular elements converge and unite to prolong backward the symphysial part of the lower jaw. In the following it will be shown that these are the opercular elements.

In discussing the lower jaw of the *Anomodontia* (**6,** p. 80), Broom adds the following to our knowledge of this part:—The opercular elements form a sort of axis round which the dentaries are built up. That part of the angular, which forms a process directed downwards and backwards, rests with its upper edge on the articular and the surangular. The articular forms a considerable part of the inner side of the posterior third of the jaw. When the jaw is viewed from the outer side the greater part of the articular is hidden by the surangular and the angular. Essentially the same is said of the lower jaw of *Oudenodon.*

Jaekel gives a figure of the lower jaw of a *Dicynodon* in "Die Wirbeltiere," p. 190. Judging by the dental end, this must be an outside view of the right ramus. According to the explanation given under the figure, an opercular and a complementary are in this way visible behind the dentary. As will be seen from the following description, I cannot agree with this interpretation.

According to Watson (**8,** p. 288), the articular is fused with the surangular. The outer face of the combined bones is largely covered by the angular, which is divided by a notch. The articulating surface of the articular and the inner side of the jaw are unknown, but there is definite evidence of the presence of an opercular.

From these abstracts it will be seen that only very little indeed has been made known on this subject, and even that "facts" recorded on one occasion were contradicted on another, and sometimes by the same author. Therefore I think to have done sufficient justice to the different authors in the above, and will abstain from further references, except where necessary for completeness.

Literature.

1.—Owen, R. ... ... "Report on the *Reptilian* Fossils of South Africa. Part 2. Description of the Skull of a Large Species of *Dicynodon* (*D. tigriceps*, Ow.), transmitted from South Africa by A. G. Bain, Esquire." Reprint from Trans. Geol. Soc. of London, 2nd. Ser. Vol. VII, pp. 233-240, Pl. XXIX-XXXII. (Read 16th May, 1855.)

2.—Huxley, T. H. ... ... "On Some *Amphibian* and *Reptilian* Remains from South Africa and Australia. 2.—On a New Species of *Dicynodon* (*D. Murrayi*) from near Colesberg, South Africa; and on the Structure of the Skull in the *Dicynodonts.*" Quart. Journ. Geol. Soc. London, Vol. 15, pp. 649-658, Pl. XXII, XXIII; London, 1859.

3.—OWEN, R. ... ... "On Some *Reptilian* Fossils from South Africa." Quart. Journ. Geol. Soc. London, Vol. 16, pp. 49-62, Pl. I-III; London, 1860.

4.—OWEN, R. ... ... "On the *Dicynodont Reptilia*, with a description of Some Fossil Remains brought by H.R.H. Prince Alfred from South Africa, November, 1860." Reprint from Phil. Trans. 1862, pp. 455-462, Pl. XIX-XXII. (Read 20th February, 1862.)

5.—OWEN, R. ... ... "Descriptive and Illustrated Catalogue of the Fossil *Reptilia* of South Africa in the Collection of the British Museum." London, 1876. XII, 88; I-LXX.

6.—BROOM, R. ... ... "On Some Points in the Anatomy of the *Anomodont* Skull." Rec. Albany Mus., Vol. I, Pt. II, pp. 75-82, Pl. IV, fig. 5. Grahamstown. Issued 18th March, 1904."

7.—JAEKEL, O. ... ... "Die *Wirbeltiere*." Berlin, 1911. 252.

8.—WATSON, D. M. S. ... "The Skeleton of *Lystrosaurus*." Rec. Albany Mus., Vol. II, Pt. IV, pp. 287-295, Pl. XV, XVI. Grahamstown. Issued 26th March, 1912.

The Dentary.—The dentaries fuse in the symphysis, of which they form the greater and upper part. The fore part of the symphysis is convex both vertically and transversely, and shows two parallel, longitudinal grooves (fig. 3). These grooves divide the symphysis in three parts, which end upwards, according to HUXLEY, in three projections, fitting into the grooves on the palatal surface of the premaxillary (see p. 1). This, however, could not be confirmed, as the extreme end of the symphysis in our specimen is damaged. The inner surface of the symphysis forms a deep, longitudinal groove, slightly inclining backwards between the upper borders of the rami of the jaw. This surface bends down vertically where the rami part from each other to diverge backwards. It then shows in its upper part a narrow pit, of which the axis is directed forwards, and below this a much broader excavation, formed by the opercular elements, the axis of which is also directed forwards (figs. 2 and 17). The suture of the opercular elements with the upper bones enters into the upper pit.

The dentaries have broad upper borders, which form the sides of the symphysial groove. These borders are thickest at the back end of the symphysis (figs. 14, 16, 17); they become only slightly thinner forwards, but gradually diminish to half this thickness from this point backwards. Two ridges extend longitudinally parallel over the whole length of the border (fig. 16). The inner ridge is well developed in front, but diminishes gradually in height backwards until it reaches the greatest thickness of the border; the height increases from this point backwards. The hind part of this ridge passes on to the complementary element. The front end of the outer ridge is merely an acute

edge between the outer and upper surfaces of the border. It rises, however, to a high and acute wall, after passing the broadest part of the border, and continues up to the end of the dentary. The hind end of the groove between these ridges is situated on the complementary.

There is a depression on the outer surface of the dentary near the symphysis, which accommodates the corresponding canine of the upper jaw when the mouth is closed. This depression runs parallel with the front surface of the symphysis, and extends from the upper border downwards and backwards till near the lower one. The described position of this depression seems to me to be the normal one, corresponding with a more or less vertical position of the occipital plate. When this condition has been complied with the alveolus of the canine inclines downwards and forwards under an average angle of 45 degrees. To fit into the depression of the lower jaw the end of the canine must therefore curve backwards. Those cases where the canine passes abruptly over the ridge, dividing the symphysial outer surface from the outer surface of the dentary, or which, generally speaking, do not comply with the above conditions, must be strongly distrusted, for there is every reason to believe that they have suffered through fossilization.

In the upper front part of this depression there is a small ridge, parallel to the ridge between the outer surfaces of the symphysis and the dentary and separated therefrom by a deep and narrow groove. This ridge originates at the upper border and passes downwards to near the middle of the depression. The deepest part of the depression is situated directly behind this ridge.

The hind part of the dentary is deeply notched by a vacuity in the jaw, the upper projection forming the whole upper border and surrounding with the lower projection the fore end of the vacuity. The upper border of the vacuity is slightly convex downwards; the fore end strongly concave backwards. The lower projection is the shortest, and terminates in a point covering the outside of the angular. The upper projection retains the same breadth up to its end at the hinder end of the vacuity, where it reaches the visible surface of the surangular, just above the upper connection of the two parts of the angular.

The Angular.—This is the first bone following on the dentary on the outside. It is already distinguishable in front of the lower end of the canine depression on the dentary (fig. 3). In this region it is a very high and thin bone (figs. 14, 16), of which the outer surface is covered by the dentary and the inner surface by the opercular. The narrow lower border only remains free. The height of the bone diminishes quickly backwards and becomes a minimum below the centre of the vacuity in the jaw. The outer surface of the angular is hollow from this point forwards, thus accommodating the lower projection of the dentary (fig. 1). The lower border of the bone is broadest where the height is a minimum. The outer surface expands fan-like from this point backwards. It forms a narrow process towards the hinder end of the upper projection of the dentary, which process there broadens into a thin vertical plate. Another process is formed at its lower border. This starts in front of the hinder end of the vacuity in the jaw, and is united inwardly to the lower border of the inner vertical part of the bone. The extreme end of the process is, however,

not in connection with this part. A vertical section over the upper and lower connections of the two parts of the angular will make their position clear (fig. 13).

The outer part of the angular continues backwards past the connecting portions, but does not reach the protruding border of the articulation surface (see also fig. 10). Its hinder border is smooth and convex backwards (fig. 4). The surface of this part of the bone is slightly convex outwards, but that part of the surface formed by the lower process is strongly concave behind, becoming less so towards its fore end.

The inner part of the angular is a thin vertical plate which covers the outside of the surangular. It is continued downwards to the lower border of that part of the jaw, also behind the outer portion of the angular, but the two parts are here divided by an opening. The lower border is connected by suture with the parallel prearticular; the hinder border in the same way with the surangular (figs. 5, 8, 10).

The Surangular.—Only two small parts of this bone are visible from the outside, one in the upper hind corner of the vacuity in the jaw and the other along the upper and hinder border of the inner part of the angular (fig. 1). An inside view shows the greater part of the bone between the articular and the complementary, forming the whole upper border of the inner end of the vacuity in the jaw (fig. 2). The prearticular and the complementary meet further forwards, and the surangular disappears behind these bones in the Meckelian cavity, wherein it may be followed far forwards (figs. 9, 15).

The bone has the shape of a wedge directly behind the dentary (figs. 8, 10). The border of this wedge forms the upper border of the jaw, and, starting directly behind the dentary, projects at right angles over the upper and hinder border of the inner portion of the angular. This projecting part of the surangular is broadest under the articulation surface. This wedge-shaped part is situated between the articular on the inside and the angular on the outside, behind the end of the inner opening of the vacuity in the jaw. It wedges so far in between these bones as to nearly reach their suture on the lower border of the jaw. This height diminishes further backwards.

The suture with the articular runs from the upper, hinder corner of the inner opening of the vacuity in the jaw upwards and backwards until it reaches the edge between the inner and upper surfaces of the ramus (fig. 6). The upper surface here, in front of the articulation surface, is concave, and the suture passes through this concavity and backwards to its outer edge. The outer border of the ramus is much thicker from this point backwards than forwards, the latter part consisting of a single sharp edge formed by the surangular and the former of two sharp edges separated by a parallel groove. These two are situated the one above the other, and are formed respectively by the articular and the surangular (fig. 5). The suture between surangular and articular runs through the groove, though not through its deepest part, but more on the side of the lower ridge. The surangular is here only a thin plate which lies against the lower surface of the articular (figs. 11 and 12). There was no suture to mark the end of the surangular here.

The Articular and the Prearticular.—The hinder border of the inner opening of the vacuity in the jaw is formed by the articular.

It is still free here, but only a very small distance backwards it coalesces with the prearticular, and then the two bones cannot be separated any more (figs. 8, 10). The suture of this coalesced bone with the angular can be traced till the end of the last. The hinder portion of this suture is very complicated (figs. 11, 12). Here two ridges are developed by both elements. The outer ridge of the coalesced prearticular is situated between the two ridges of the angular, while the inner ridge of the angular fits in between the two of the coalesced bone. These ridges become less prominent forwards, except the outer ridge of the angular, which passes into the high vertical side of the inner portion of this bone.

The articulation surface of the coalesced articular has a high front margin, which passes into the uppermost of the already mentioned two ridges on the outer border (fig. 5). This upper ridge passes in its turn into a high back margin, which crosses the upper surface of the coalesced bone from the outer border inwards and backwards (fig. 7). This margin is still visible on the inner surface till just below the inner process (fig. 6).

There is a process from the inner surface of the bone at about equal distances from the upper and lower border. Its longest dimension is parallel with the larger articulation surface. Its upper surface is convex, and forms part of the articulation surface. The lower surface of this process is slightly concave at the back, and its free edge is sharp (figs. 2, 6, 11, 12).

The coalesced bone forms another process downwards, being the extreme end of the ramus. This process has a triangular section, of which the outer angle is the most acute (figs. 5, 6, 7).

The articulation surface consists of three parts: an upper surface, a vertical surface, and the upper surface of the inner process (figs. 7, 11, 12). The upper and vertical surfaces meet in a ridge, which is convex upwards and inwards. The angle between the upper and vertical surfaces is acute; the one between the vertical surface and the upper surface of the inner process is right.

The upper surface is convex in a backwards-forwards direction, and concave from the outer to the inner edge. The vertical surface is convex inwards.

The prearticular continues forwards from the hinder border of the inner opening of the vacuity in the jaw, forming the whole lower border of this opening, and then disappearing behind the opercular (figs. 2, 10, 13, 14, 15, 16). It has been followed behind this element till above the place where the angular disappears between the opercular and the dentary. Before reaching the opercular it is in touch with that part of the dentary which might be allocated to the lower end of the complementary.

A ridge runs near and parallel to the lower border of the bone on its outer surface (in the Meckelian cavity, fig. 10). The height of this ridge increases towards the back, and it also rests there on a ridge of the angular, which on this element runs parallel with and a little above the lower border. The suture of the angular with the coalesced part of the prearticular has already been described (figs. 11, 12).

The articular is still a separate bone directly behind the inner opening of the vacuity of the jaw. Just a few millimetres further backwards it coalesces with the prearticular. The exact relation of the two parts is thereby totally obliterated, but it is still possible to

identify certain portions of the coalesced bone with the composing parts. It seems to me, for example, that the downward process of the coalesced bone is part of the prearticular, and this for the following two reasons: The ridges of the separate part of the prearticular increase in height backwards, and it is therefore very probable that the bone forming the intricate suture behind also belongs to the prearticular. The high margin of the articulation surface behind gives the impression that this is the end of the articular. I therefore presume the original boundaries of the bones to have been as indicated in figs. 5, 6, and 7.

The Opercular.—The opercular elements are situated in the distal part of the jaw. They are coalesced in the symphysis (figs. 2, 16, 17). Directly behind the symphysis they occupy about two-thirds of the height of the jaw (fig. 14), but they gradually diminish in height towards the back till near the inner opening of the vacuity in the jaw. Here the end is divided into two unequal parts by a longitudinal notch. The upper part covers a small portion of the inner surface of the prearticular, and then breaks off abruptly. The lower part, which ends in a point, is situated below and a little to the outside of the prearticular. The opercular is thinnest behind, and becomes gradually thicker forwards, the angular at the same time thinning out. There is a groove in the upper border of the opercular towards the symphysis, accommodating the lower border of the inner wall of the dentary (figs. 14, 16). The narrow pit on the border of the operculariа and the dentaries in the symphysis continues forwards through two-thirds of the symphysis, and then bends sharply upwards, parallel with the front surface of the symphysis (fig. 1). A triangular surface of the coalesced operculariа is visible in front at the lower end of the symphysis (fig. 3).

The Complementary.—There is no separate bone which can be taken to be the complementary. It appears to me, however, that the bone has coalesced with the hinder end of the inner wall of the dentary (fig. 2). There is a separation in this region in one specimen between a thin plate which clearly belongs to the dentary and a broad inner part which bears the continuation of the groove on the dentary (fig. 9). It could not be made out whether this separation is a suture or a fracture. The other ramus does not show this separation. An examination of many other specimens on this point gave no result. This investigation, however, rose the presumption that the complementary could very well have coalesced with the inner wall of the dentary, the hinder part of which forms a very obtuse angle with the fore part. Definite proof of the presence of a complementary has, however, not been obtained.

Dimensions.—The following dimensions were taken from Pal. Cat. No. 3099 (figured in figs. 1-4, and 9):—

Length of the left ramus	105 mm.
Height of the symphysis	45 mm.
Height of the left ramus over the centre of the outer opening of the vacuity	36 mm.
Length of the left dentary	73 mm.
Length of the left outer opening of the vacuity ...	34 mm.
Length of the left inner opening of the vacuity ...	41 mm.
Length of the visible outer portion of the angular	60 mm.
Length of the visible surface of the operculariа on the outer surface of the symphysis	14 mm.

Explanation of Plates.

(Figures all of natural size.)

Lower Jaw of *Lystrosaurus*.

Fig. 1. Outside view of the left ramus. Pal. Cat. No. 3099.
Fig. 2. Inside view of the left ramus. Pal. Cat. No. 3099.
Fig. 3. The symphysis seen from in front and below. Pal. Cat. No. 3099.
Fig. 4. Undamaged hinder end of the outer portion of the angular. Pal. Cat. No. 3099.
Fig. 5. Outside view of an undamaged left hinder end of a jaw. Pal. Cat. No. 3098.
Fig. 6. Inside view of the same specimen.
Fig. 7. Back view of the same specimen.
Fig. 8. Section of the left ramus of a jaw behind the inner opening of the vacuity. Same specimen.
Fig. 9. Section of the left ramus of a jaw just in front of the hinder end of the dentary. Pal. Cat. No. 3099.
Fig. 10. Series of sections of a left ramus. Pal. Cat. No. 3097. Going backwards from left to right. The distances of every two sections are put between them.
Fig. 11. Section of an articulation part of a right ramus. Pal. Cat. No. 3096.
Fig. 12. Section of the same specimen a little further backwards.
Fig. 13. Section of the left angular across the connections of the two parts. Pal. Cat. No. 3095.
Fig. 14. Section of a jaw near the symphysis. Pal. Cat. No. 3095.
Fig. 15. Section of the left ramus of the jaw of the same specimen a little further backwards, showing the intricate suture of the angular and the opercular at this point.
Fig. 16. Section of a jaw showing the united opercularia. The angularia are still present. Pal. Cat. No. 3094.
Fig. 17. Section of the same specimen a little further forwards.

An. = angular.
Ar. = articular.
C. = complementary.
D. = dentary
M.C. = Meckelian cavity.
Op. = opercular.
Pa. = prearticular.
Qa. = quadrate.
Sa. = surangular.
x. = a saw cut.
i.o. = inner opening of the vacuity in the jaw.

After the above was written and ready for the printer, I, for the last time, looked up the available literature and found a paper by Mr. D. M. S. Watson, "On some *Reptilian* Lower Jaws," in the Ann. and Mag. of Nat. Hist. London, Ser. 8, Vol. 10, No. 60, Dec. 1912, which for reasons outside my power had escaped my notice. To my great astonishment I saw that the description of the lower jaw of the *Anomodontia* did not agree with my observations on the *Lystrosaurus* jaw. The most marked difference between the two descriptions is that Watson finds a separate coronoidal element between the dentary and the complementary, a bone which the closest scrutiny of my *Lystrosaurus* jaws did not reveal. Further, Watson's specimen did not show the inner opening of the vacuity in the jaw nor the canal in the symphysis. Also the arrangement of the bones around the much

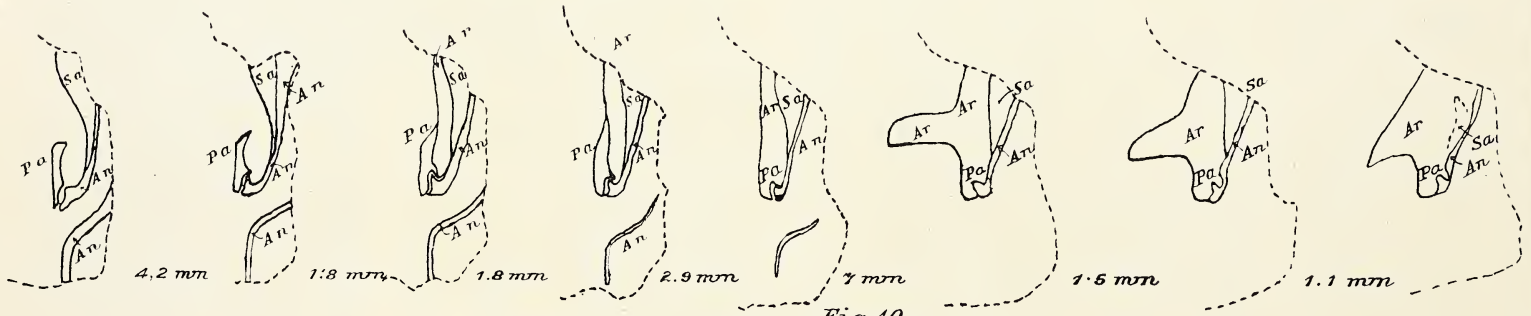

Fig. 10

smaller opening of the vacuity was different to what I had found around a much bigger opening. It occurred to me that the above-mentioned differences might have to be attributed to the fact that we had described the jaws of different genera. A lower jaw of a *Dicynodon* was thereupon developed to see whether this explanation would hold good. It appeared, however, to be in detail exactly like the jaw of *Lystrosaurus* described above. I can therefore definitely state that the alleged coronoidal element between the dentary and the complementary **does not exist** in *Lystrosaurus* nor in *Dicynodon*. My other observations which differ from WATSON's description are also sufficiently supported by proof in the above, and further discussion would only mean repetition. I would only further draw the attention to the differences in the description of the dentary, the complementary, the surangular, the angular, and the articular.*

* The mail just brings the latest issue of the "Ann. and Mag. of Nat. Hist.," London, ser. 8, vol. 14, No. 79, July, 1914, which contains a paper by D. M. S. WATSON, "*Dicynodon Halli*, sp. n., an *Anomodont Reptile* from South Africa." It is herein stated on p. 97, that the lower jaw of this specimen served for the description of the lower jaw of the *Anomodontia*, mentioned above. Also that the apparent suture between the dentary and the coronoid, although clear as a very fine dark line in this specimen and several others, is perhaps something else. I would here like to refer back to my remarks on p. 2.